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Plant traits, biotopes and urbanization dynamics explain the survival of endangered urban plant populations

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Abstract

1. With accelerating urbanization, the urban contribution to biodiversity conservation becomes increasingly important. Previous research shows that cities can host many endangered plant species. However, fundamental questions for urban nature conservation remain open: to what extent and where can endangered plant species persist in the long term and which mechanisms underlie population survival?
2. We evaluate the survival of 858 precisely monitored populations of 179 endangered plant species in Berlin, Germany, by assessing population survival throughout different urban ecosystems over a period of 7.6 years on average. By linking population survival to various landscape variables and plant traits, we unravel the underlying drivers.
3. More than one–third of populations went extinct during the observation period. Population survival was inversely correlated to the increase in impervious surfaces in the vicinity following the first 11 years after the fall of the Berlin wall. Additionally, populations in semi-natural habitats like forests and bogs were surprisingly more prone to local extinction than populations in anthropogenic habitats. Survival was highest for competitive species with a preference for drier soils (Ellenberg indicator for soil humidity).
4. *Synthesis and applications*. Considerable levels of local population extinction demonstrate that the presence of endangered plants cannot be directly linked with their long-term survival in cities. However, the survival of remaining populations indicates opportunities for urban biodiversity conservation both within and outside conservation areas. The elucidated links between population survival, urbanization dynamics, biotope class and species traits support urban conservation strategies that reduce the proportion of impervious surface, prioritize conservation management in forests and grasslands and explore the opportunities of green spaces and built-up areas.

KEYWORDS

anthropogenic biotopes, biodiversity conservation, endangered plant species, plant traits, population monitoring, population persistence, urban ecosystems, urbanization changes

1 | INTRODUCTION

As urbanization accelerates globally, the question of the urban contribution to biodiversity conservation is becoming increasingly important (Kowarik & von der Lippe, 2018; McKinney, 2002; Nilon et al., 2017; Parris et al., 2018). The number of urban conservation studies has risen sharply in recent years (Shwartz, Turbé, Julliard, Simon, & Prévot, 2014) and indicate considerable opportunities for biodiversity conservation. Indeed, cities can be very rich in native species (Aronson et al., 2014), including a considerable richness of endangered plant species as reported from cities in Africa (Rebelo, Holmes, Dorse, & Wood, 2011), Asia (Wang et al., 2007), Australia (Ives et al., 2016), Europe (Kowarik & von der Lippe, 2018) and North America (Lawson, Lamar, & Schwartz, 2008). From these insights, a narrative regarding cities' contribution to biodiversity conservation has developed, and with this several strategies to promote urban biodiversity have been suggested. Classical approaches such as the designation of protected areas are increasingly complemented by integrative approaches arguing for a biodiversity-friendly management of green spaces (Aronson et al., 2017; Chollet, Brabant, Tessier, & Jung, 2018), a reconciliation of urban land use and biodiversity conservation (Elmqvist et al., 2013), the integration of biodiversity in urban design (Garrard, Williams, Mata, Thomas, & Bekessy, 2018) or the promotion of urban wilderness (Hwang, Yue, Ling, & Tan, 2019; McKinney, Kowarik, & Kendal, 2018).

However, strategies to promote urban biodiversity in general may not specifically support the protection of endangered plant species. While target species conservation is a major motive for urban biodiversity conservation (Dearborn & Kark, 2010), the meta-analysis by Shwartz et al. (2014) revealed that empirical evidence for the effectiveness of urban conservation strategies is lacking. It therefore remains unclear which criteria should guide the allocation of scarce resources for urban nature conservation or whether the contribution of cities to the conservation of biodiversity is generally overestimated (Shwartz et al., 2014). An assessment of the long-term survival of endangered plant species in cities is currently hampered by knowledge deficits in three key areas.

1.1 | Population persistence

The occurrence of species of conservation concern in cities does not necessarily indicate their effective protection (Shwartz et al., 2014). Environmental constraints due to urban land use, fragmentation or novel environmental stressors represent significant limitations on plant dispersal and recruitment (Kowarik & von der Lippe, 2018; McDonnell & Hahs, 2015; Williams et al., 2009), while habitat loss and change can be responsible of local plant extinctions (Duncan et al., 2011; Knapp, Kühn, Stolle, & Klotz, 2010). Thus, population persistence is a key issue for sustainable target species conservation in cities, as there is evidence for decreasing population sizes in urban plants over time (Chocholoušková & Pyšek, 2003; Knapp et al., 2010), and remaining populations of a species can thus mask future extinction debts (Hahs & McDonnell, 2014). However, most urban biodiversity studies report as snapshot studies the occurrence of species at a certain point in time, but do not allow conclusions to be drawn about the persistence of urban populations (but see Lawson et al., 2008; Schwartz, Smith, & Steel, 2013).

1.2 | Type of habitat

While the occurrence of target species of conservation concern across different habitats in cities has often been described, the relative importance of different urban habitats for such species is not fully understood (Shwartz et al., 2014). Species of conservation concern have been reported from very different habitat types within cities (Planchuelo, von der Lippe, & Kowarik, 2019), for example, forests (Godefroid & Koedam, 2003), brownfields (Bonthoux, Brun, Di Pietro, Greulich, & Bouché-Pillon, 2014), parks (Cornelis & Hermy, 2004) or cemeteries (Kowarik, Buchholz, von der Lippe, & Seitz, 2016; Löki, Deák, Lukács, & Molnár, 2019). However, an important bias is that populations of endangered species have not been studied equally across all urban habitat types. Rather, most urban conservation studies address larger habitats (roughly >2 ha), with natural remnants and large green spaces being overrepresented (Shwartz et al., 2014). Moreover, species inventories of urban nature reserves are likely better known than those of unprotected land use types.

1.3 | Environmental and urbanization predictors

Which species occur in urban habitats not only depends on local habitat features such as patch size but also on features of the surrounding urban matrix as indicated by urbanization parameters (e.g. the proportion of impervious surface, human population density) or the vicinity to (semi-)natural ecosystems. Previous urban studies have revealed the relative importance of many potential predictors of species richness (e.g. Anderson & Minor, 2019; Beninde, Veith, & Hochkirch, 2015; Westermann, von der Lippe, & Kowarik, 2011; Williams, Morgan, McCarthy, & McDonnell, 2006). However, results based on total species richness cannot necessarily be generalized to endangered plant species, as shown for urban grassland reserves in Prague (Jarošík, Konvička, Pyšek, Kadlec, & Beneš, 2011). Specific analyses for endangered plant species are rare and yielded ambiguous results: studies at larger national scales revealed positive relationships between urbanization parameters and species of conservation concern (Kühn, Brandl, & Klotz, 2004; Lenzen, Lane, Widmer-Cooper, & Williams, 2009; Shwartz, Muratet, Simon, & Julliard, 2013), while studies at smaller city scales yielded contrasting results (Schmidt, Poppendieck, & Jensen, 2014). However, many studies rely on heterogeneous urban landscapes (e.g. grids) without specifying the habitat scale, that is, the specific locations of endangered plant populations. Moreover, dynamics of urban environments are an important features of cities (Ramalho & Hobbs, 2012). Change

rates of urbanization measures (e.g. impervious surface, population size) can determine urban biodiversity patterns (Fischer, Rodorff, von der Lippe, & Kowarik, 2016). Such measures are rarely incorporated into analyses of the long-term survival of endangered species, although dynamic changes of urban environments can potentially threaten population survival, for example, by loss of open spaces, or indirect urbanization effects.

1.4 | Species traits

Besides characteristics of a population's environment, species identity or more generally, species traits, are held responsible for the vulnerability to local extinction in cities (Duncan et al., 2011). Although several studies have indicated shifts in specific plant traits due to urbanization, there was only a marginal impact of species traits on plant extinctions in another study (Duncan et al., 2011). However, higher frequency in urban habitats has been linked to competitive traits (e.g. plant height; Fischer, von der Lippe, & Kowarik, 2013) or strategies (Chocholoušková & Pyšek, 2003), and to preference for nutrient-rich sites (Knapp et al., 2009), while lower frequencies in cities are reported for species with high water requirements (Knapp et al., 2010).

We aimed to elucidate the persistence of endangered plant species in cities—and underlying mechanisms—by evaluating a unique dataset from Berlin. These data contained long-term monitoring results of a large number of precisely mapped plant populations (n = 858) belonging to 179 endangered plant species. These plant species have been identified as priority species of conservation concern in Berlin's Flora Protection Program and the extant populations of these species have been subjected to a repeated monitoring (Meißner & Seitz, 2010). Therefore, information was available on which populations have survived or have gone locally extinct at the respective sites since the first survey.

To unravel mechanisms that might underpin population survival, we assigned each of the originally mapped populations (a) to a specific biotope type and (b) characterized the site occupied by each population by a range of urban landscape variables whose fundamental relevance has been shown previously and that were related to habitat features, the urbanization of the surroundings and the vicinity of (near)-natural ecosystems. Additionally, we linked population survival to plant traits that have been shown to be relevant to plant performance in previous urban studies.

We expected population survival rates to decrease with increasing urbanization or rapid changes in the areas surrounding each population and to differ significantly among biotope types. We assumed a positive correlation between population survival and an increasing proximity to natural remnants or large forest and grassland areas, which might act as propagule sources. Furthermore, we expected a positive relationship between plant traits related to competitive ability and population survival.

In detail, we addressed the following research questions: How is the survival rate of populations of endangered plant species in Berlin related to (a) features of the respective habitats (e.g. type of biotope, patch size, legal conservation status); (b) the degree and dynamics of urbanization of the surrounding urban matrix (e.g. current share and change in impervious surface area, human population density); (c) to the vicinity of (near)natural ecosystems (e.g. distance to natural remnants, proportion of forests in buffer around the sites) and (d) plant functional traits of the respective endangered plant species (e.g. Ellenberg indicators, CSR strategy).

2 | MATERIALS AND METHODS

2.1 | Study area

This study was carried out in Berlin, the largest city of Germany, with 3.6 million inhabitants in 2017. Berlin is a typical large European city, including a wide range of ecosystems ranging from remnants of semi-natural and agrarian landscapes or urban greenspaces with different land use histories to novel ecosystems in vacant urban-industrial land. Green and blue spaces make up 41% of the total area of Berlin, which is 891 km^2; the remaining 59% is covered by built-up and traffic areas (SenStadtUm, 2016). Red lists of endangered species were established in the 1980s and updated several times since. From today's perspective, we thus know that 17% of Berlin's flora has gone extinct since the mid-19th century, and 29% is currently being endangered (Seitz, Ristow, Meißner, Machatzi, & Sukopp, 2018).

2.2 | Population data

We used an extensive monitoring dataset from Berlin's Flora Protection Program (Berliner Florenschutzkonzept) on the precise geographical location of 858 populations of 179 endangered plant species in Berlin (see Appendix S1). From these, 72.5% of the species are herbaceous, 20.6% geophytes, 3.5% shrubs, 1.9% hydrophytes and 1.5% trees (Table 1). The 10 most populous plant families are, in decreasing order, Rosaceae, Cyperaceae, Caryophyllaceae, Asteraceae, Poaceae, Orchidaceae, Ranunculaceae, Iridaceae and Fabaceae (Table 1). The monitored species have the highest conservation priority because they are threatened locally and/or at regional, national or global scales (Meißner & Seitz, 2010). A population was discerned from another when individuals where separated at least 30 m or when populations were clearly separated by roads or paved paths. We used the dataset in previous studies (Planchuelo, Kowarik, & von der Lippe, 2020a; Planchuelo et al., 2019) but here include for the first time information on population survival. The first inventory of populations was compiled from several expert surveys after 1990. On the basis of the georeferenced locations of this initial dataset, a re-mapping project took place between 2009 and 2014, aiming to relocate all previously mapped populations. The average period of time between the first and second mapping of a population was 7.6 (±0.2) years. This allowed us to differentiate persistent from

locally extinct populations of those recorded in the initial dataset. To avoid methodological bias, we excluded all populations from the initial compilation with imprecise information on the spatial location, and populations in open waters, due to difficulties in relocating and resurveying them.

TABLE 1 Number of populations and species belonging to different life forms and to the 10 most populous plant families of the endangered plants used in our study

	Number of populations		Number of species	
Life form				
Herbaceous perennial	566	66.0%	101	56.4%
Geophyte	177	20.6%	30	16.8%
Herbaceous annual	56	6.5%	23	12.8%
Shrub	30	3.5%	15	8.4%
Hydrophyte	16	1.9%	9	5.0%
Tree	13	1.5%	1	0.6%
Plant family				
Rosaceae	96	11.2%	13	7.3%
Cyperaceae	89	10.4%	15	8.4%
Caryophyllaceae	84	9.8%	11	6.1%
Asteraceae	83	9.7%	21	11.7%
Poaceae	73	8.5%	13	7.3%
Orchidaceae	47	5.5%	8	4.5%
Ranunculaceae	44	5.1%	10	5.6%
Iridaceae	35	4.1%	1	0.6%
Fabaceae	28	3.3%	6	3.4%

2.3 | Habitat features

To evaluate the role of different biotope types for population survival, we intersected the location of each mapped population with the respective biotope class from the Berlin biotope mapping (SenStadtUm, 2014). Terrestrial populations of endangered plant species were present in eight major biotope classes (Figure 1): forests, grasslands, ruderal sites, built-up areas, bogs and marshes, groves and hedges, green spaces and agricultural fields. We calculated the area of the respective biotope patches to elucidate the role of patch size for population survival.

To test for the role of the legal protection status of an area on population survival, we attributed the site of each population to one of the following categories: nature reserve (*Naturschutzgebiet*), Natura 2000 site, protected landscape (*Landschaftsschutzgebiet*) and unprotected sites. The first three categories represent legally protected areas, with decreasingly strict protection status and management measures. We also assessed whether the populations were located in former East Berlin or West Berlin to evaluate if the different patterns of urban development in both parts of the city had an effect on population survival.

2.4 | Landscape variables

We determined several characteristics of the urban matrix surrounding the populations of endangered plants and used them to reveal the effects of urbanization on population survival (see Appendix S2 for parameters and sources). We calculated data on the proportion of impervious surface, the mean floor space index (a measure of urban

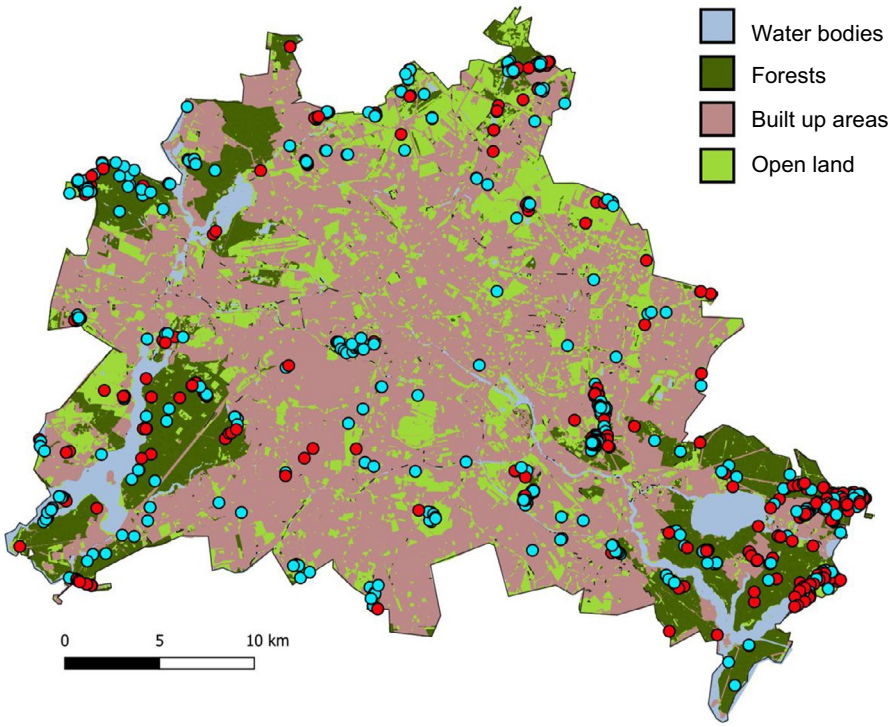

FIGURE 1 Location of populations (n = 858) of endangered plant species in Berlin that survived (blue dots) or did not survive (red dots) during the monitoring period. The category 'open land' includes biotope classes that were further differentiated in the analyses

density, i.e. the ratio of a buildings total floor area and its lot area), human population density and the length of the road network in a 500 m radius buffer surrounding each population of endangered plant species. To account for effects of spatial isolation from (near)natural ecosystems, we calculated the proportion of forests and grasslands for a 500 m radius buffer around each population, based on information from the Berlin biotope map (SenStadtUm, 2014).

To account for urbanization dynamics throughout the monitoring period, we calculated the changes in the proportion of impervious surface area throughout two periods of time (i.e. 1990–2001 and 2005–2016) for a 500 m radius buffer around each population. These periods reflect different phases of urbanization: the first decade after the fall of the Berlin Wall in 1989, and a period of less dynamic but progressive urban development. Both periods are covered by citywide measurements of the impervious surface area using the same method. As a measure of socioeconomic change, we compiled mean human population constancy (i.e. the percentage of residents living at least 5 years in the same address) in the same buffer from the Berlin map of land use (SenStadtUm, 2016).

To calculate the average values of each parameter, we spatially intersected the corresponding map with each individual buffer in QGIS (2019) and then used the plugin 'Dissolve with Stats' to obtain the average values for each buffer. The distance of each population to the nearest road and to the nearest natural remnant was calculated in QGIS (2019) with the 'NN Join' plugin. We addressed those biotopes as natural remnants if they corresponded to historical natural ecosystems, being only slightly affected by human impacts, following the classification by Kowarik and von der Lippe (2018). Such remnants include mires, wetlands, semi-natural forests and some semi-natural grasslands. Spatial information on natural remnants was derived from Planchuelo et al. (2019). Appendix S3 summarizes the methodological approach of the study.

2.5 | Plant traits

Plant traits, CSR strategy types (Grime, 1977) and Ellenberg indicators (Ellenberg, Weber, Düll, Wirth, & Werner, 1991) have been successfully linked to urban biodiversity patterns in previous studies (Williams, Hahs, & Vesk, 2015). We thus included these parameters as predictors of population survival in our analyses (Appendix S4). Information on plant morphological traits (SLA, plant height) and the CSR strategy of the species was gathered from the BIOFLOR database (Klotz, Kühn, Durka, & Briemle, 2002). For information on the realized niche of a species, we used indicator values for the soil humidity, soil nitrogen and soil acidity requirements, and for light and temperature requirements of each species from Ellenberg et al. (1991).

2.6 | Statistical analyses

To relate population survival to habitat characteristics and landscape variables (Appendix S2), we used a GLMM (R function glmer; Bates, 2010). We coded population survival as a binomial response and corrected for spatial and phylogenetic dependence by including the spatial coordinates of their locations (longitude and latitude) and plant genus as random factors. Plant genus has been included as a random factor in GLMM models to successfully account for phylogenetic dependencies (e.g. Pandit, White, & Pocock, 2014). Because of the varying period between the first and the second monitoring of the populations, this time span in years was also included as a random effect in our model. All habitat and landscape variables were tested for intercorrelation and as no correlations higher than $|r| < 0.7$ appeared, all of them were included as fixed effects in a full model (Dorman et al., 2013). A minimal adequate model was chosen by stepwise backward selection of the predictors based on minimal AIC. Random variable selection was done separately with the entire set of variables prior to backward selection of the fixed effects. We evaluated the prediction accuracy of the model by calculating the area under the receiver operating curve (AUC) with the package pROC in R (Robin et al., 2011).

To estimate the effect of plant traits on population survival and to account for possible nonlinear effects, we calculated the relative importance of each variable through a conditional random forest and successively performed a conditional inference tree analysis. For both, we used the same response as in the GLMM (binomial population survival) and the set of predictors related to the morphological plant traits of the species, their CSR strategy and their realized niche as expressed through Ellenberg indicator values (Ellenberg et al., 1991; Appendix S4). A variable selection through a conditional random forest is a machine learning technique that is able to estimate the relative importance of highly correlated predictors (Strobl, Boulesteix, Kneib, Augustin, & Zeileis, 2008). A conditional inference tree is a non-parametric type of decision tree where the dataset is recursively split into dichotomous subsets, which are discriminated by the most significant predictor (Hothorn, Hornik, & Zeileis, 2006). We chose these models because of their ability to display interactions between different traits and their flexible handling of categorical data.

All analyses were performed with the statistical and programming software R version 3.5.2 (R Core Team, 2018).

3 | RESULTS

3.1 | Survival rate

Almost two-thirds of the populations of endangered plant species (64%) mapped in the first monitoring were confirmed in the second monitoring (551 populations). Thus, more than one-third of all populations became locally extinct during the period between the two monitoring dates, which averaged 7.6 years. During that time, from a total of 179 endangered species, 49 (27%) went extinct for the study sites.

3.2 | Landscape predictors

In the binomial GLMM, changes in the proportion of impervious surface between 1990 and 2001 in a 500 m radius surrounding the populations was the variable with the strongest effect on the survival of endangered plant species, followed closely by the biotope class. Additionally, the minimal model with the best fit based on AIC selection also included distance to the nearest natural remnant as predictor, which had a negative, but non-significant effect (Table 2).

Population survival was negatively affected by changes in the proportion of impervious surface between 1990 and 2001 (Figure 2). Notably for those populations where the proportion of impervious surface decreased, population survival was considerably higher and no populations became locally extinct when impervious surface decreased below −1.6%.

The biotope class in which populations were situated was also a significant predictor of population survival. Survival rates were highest in green spaces (0.90) and built-up areas (0.78) and lowest in forests (0.58) and ruderal sites (0.61). While the first two biotope types only housed a few populations, the last two biotope types had significantly more populations. Forests hosted the majority of populations of endangered plants but had the lowest survival rate (Figure 3). Grasslands, with the second highest number of populations (261), showed an intermediate survival rate of 0.69.

The distance to a natural remnant was also a variable selected by the GLMM model as a predictor of population survival. However, modelled estimates of population survival only showed a marginal decrease on average from 0.63 at 0 m in a remnant patch to 0.59 at 1,500 m.

TABLE 2 Analysis of deviance table (Type II Wald Chi square Test) of the effects of predictor variables on population survival of endangered plant species from the minimal GLMM model after backward selection (prediction accuracy of AUC = 0.872). Statistically significant *p* values are marked in bold. Random effects of genus and monitoring duration of the endangered plant populations were retained in the minimal model

Variable	Chi square	*df*	*p* value
Changes in impervious surface 1990–2001 (500 m buffer)	4.96	1	**0.026**
Biotope class	15.30	7	**0.032**
Distance to natural remnants	2.70	1	0.100

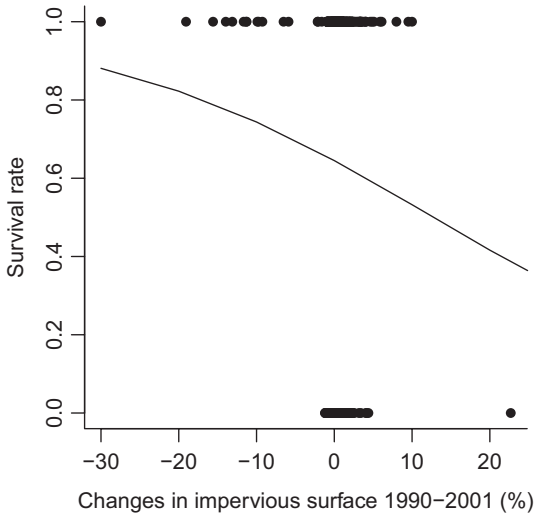

FIGURE 2 Effect of change (period 1990–2001) in the proportion of impervious surface in a 500 m buffer around 858 populations of endangered plant species on their survival rate. Dots represent actual data, while the trend line represents the predicted probabilities

3.3 | Plant traits as predictors

Calculating the relative importance of each variable through a conditional random forest revealed indicator values for soil humidity requirements and CSR strategy as most important plant traits in predicting population survival (Figure 4). In a subsequent conditional

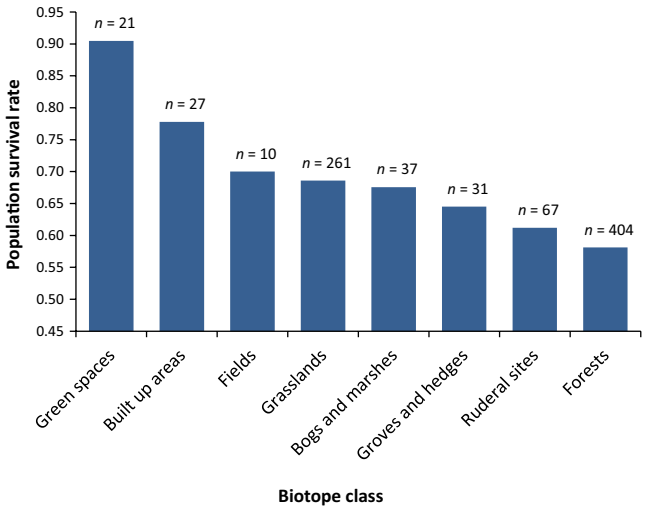

FIGURE 3 Survival rate of populations of endangered plant species (*n* = 858) across different biotope classes in Berlin over an average period of 7.6 years; *n* above the bars indicates the total number of populations in each class

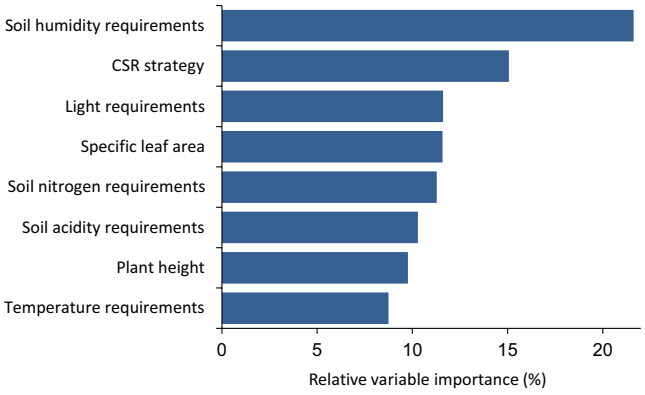

FIGURE 4 Plant traits and Ellenberg indicator values arranged by their relative importance as predictors of population survival of endangered plant species in a conditional random forest model. Each percentage represents the variability in population survival explained by each variable

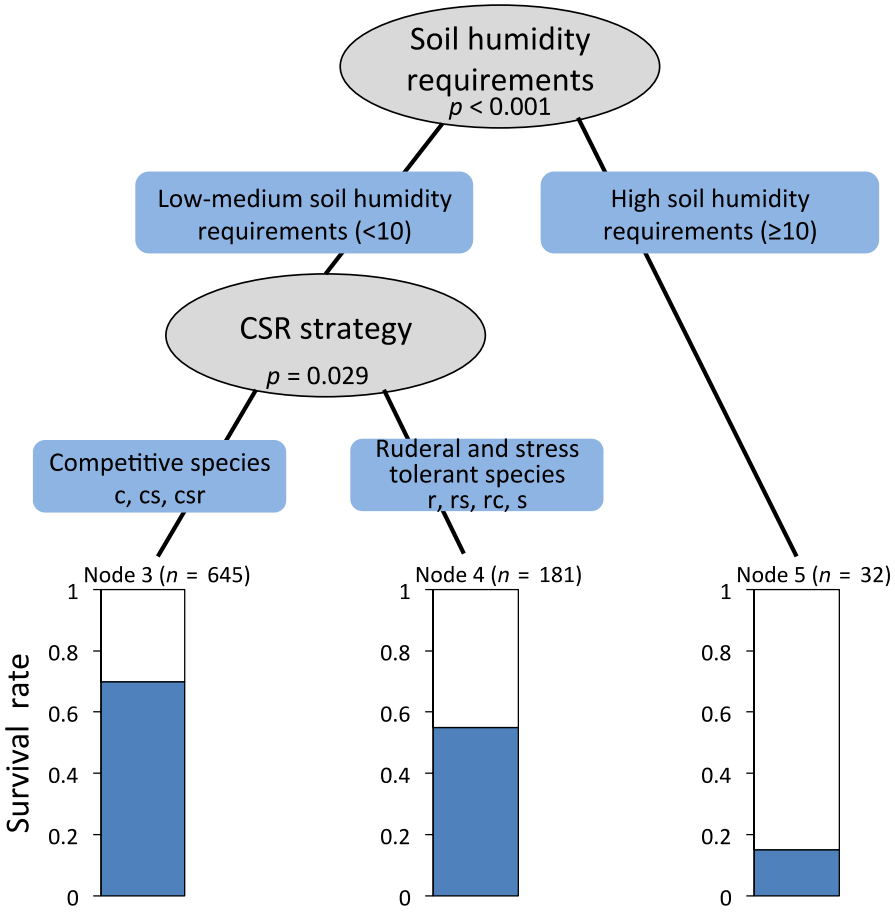

FIGURE 5 Effect of plant traits on the survival rate of populations of endangered plant species in Berlin (n = 858). The conditional inference tree shows all significant partitioning effects of plant traits and Ellenberg indicator values on population survival; n above the bars indicates numbers of populations left in each terminal node

inference tree analysis, only these two predictors were retained in the model as significant predictors of population survival of endangered plants (Figure 5). Soil humidity requirements (p < 0.001) caused the first split in the data, with an overall lower survival (0.16) in populations with the highest soil humidity requirements (≥10). Those with low to medium soil humidity requirements (<10) had overall higher survival rates and were further split according to their CSR strategy (p = 0.029), with populations of competitive species (c, cs, csr) having higher survival rates (0.69) than those with ruderal or stress tolerant (r, rs, rc, s) strategies (0.54).

4 | DISCUSSION

While cities can harbour many endangered plant species, their importance for biodiversity conservation has been challenged (Shwartz et al., 2014). This study addressed one critically understudied key question: the extent to which endangered species not only occur in cities but also survive under urban conditions. To our knowledge, this is the first long-term study to investigate the population survival for a large set of endangered plant species (179) at their respective growth sites in a big city.

A key finding is that populations of endangered plant species in urban settings can be highly dynamic and that there is a considerable risk of local extinction within a period of <10 years. At the second monitoring date, about two-thirds of the populations were confirmed. Yet, population survival as reported in this study does not necessarily relate to survival over longer periods of time, which is generally challenging in urban environments as recently reported from the low establishment rates of endangered plants in Berlin (Kowarik & von der Lippe, 2018). Therefore, our results on population survival may not reflect extinction debts—which should be verified by continued monitoring. Additionally, in the period between the first and the second monitoring, some locally extinct species may have colonized new sites due to meta-population dynamics (Loreau, Mouquet, & Holt, 2003) or population establishment from natural or human-mediated long-distance dispersal. However, our study cannot consider newly established populations at locations other than those originally surveyed. This could explain why ruderal sites and species, with fast population dynamics and high dispersal capacity, had lower than expected survival rates in our study.

As for the underlying factors of local extinction or survival of populations, our study found significant differences with regard to urbanization dynamics, biotope classes, proximity to semi-natural areas and species traits.

4.1 | Urbanization dynamics

Previous studies have shown that high levels of urbanization relate to higher risk of local extinction, as shown for native grassland plants

(Williams et al., 2006). In our study, the proportion of impervious surface around the growing sites predicted population survival. The risk of local extinction increases significantly with increasing impervious surface for the period 1990–2001 but not for the later 2005–2016 period (Table 2). These periods differed in the pace of urbanization in Berlin (SenStadtWo, 2019a). The first one covers the decade after the fall of the Berlin Wall and thus a period of rapid change, in which some old building structures were demolished and some vacant land converted to new uses. The urban development during the second period was less rapid, including a period of stagnation at the beginning and a later focus on the development of existing built structures (densification). We expect that changes within the first period affected populations of endangered species directly by habitat loss, and indirectly by changing disturbance regimes at the locations of the populations, for example, by changing recreational pressure. In the same vein, a study from Buenos Aires revealed that population growth, rather than human population density around urban parks, negatively related to plant species richness within park environments (Fischer et al., 2016). Missing significance of urbanization dynamics for population survival during the second time-period could mask extinction debts because the ecological consequences of further development only take effect later.

Urbanization and socio-economic patterns differed between West and East Berlin due to the political division of the city after the Second World War. Correspondingly, distribution patterns for fruit trees, for example, still differ today in both parts of the city (Larondelle & Strohbach, 2016). Our study, however, found no corresponding legacy effects of Berlin's history as the location of the populations in either East or West Berlin did not affect population survival. This suggests that similar mechanisms operated in both parts of the city.

4.2 | Biotope types

As assumed, biotope classes also had a pronounced effect on population survival (Table 2), with forests and grasslands hosting most populations. Surprisingly, the survival rate was lowest in forests (0.58; Figure 2a). The fact that 42% of populations of endangered plants in forests were no longer present at the second monitoring is alarming, as forests in Berlin are generally protected, that is, there is no significant loss of forest area, and today's forest management aim is to develop semi-natural forests in Berlin (SenStadtWo, 2019b). The low survival rates in forests likely relate to changes to the vegetation structure. Many of Berlin's forests had sparse canopy and shrub layers with clearings within forest-heath complexes as a consequence of being grazed for centuries until the mid-19th century (Sukopp, 1990). Forest structures became denser with the cessation of grazing, but a sparse canopy cover was preserved by increased harvesting of timber and other destructive activities during and after Second World War (Seidling, 1990). These settings had supported many species with high light requirements, adapted to the prevailing nutrient-poor sandy soils. However, during the last decades, changes in forest management (Seidling, 1990) and the establishment of native and alien species in the shrub layer (*Prunus serotina*, *Acer* species; Kowarik, von der Lippe, & Cierjacks, 2013) made forest stands denser again. Comparing vegetation relevés from 1955 and 1986 accordingly revealed a decline in many species of semi-open forest habitats (Seidling, 1990). In the same vein, mechanisms leading to denser forest structures can induce local extinctions in this study—as indicated by species' light requirements as predictor of population survival (Figure 4). Indeed, the species with the lowest survival rates in forests include *Festuca psammophila* and *Botrychium lunaria*, species which are normally missing in dense forests but that usually colonize nutrient-poor sites in open forests or grasslands. Furthermore, the increasing availability of nutrients due to influx from urban sources makes these species even more vulnerable (Knapp et al., 2010; Williams et al., 2015), exacerbating the negative effects of a lower light availability.

Conversely, the survival rate was highest in the most anthropogenic biotopes (i.e. green spaces: 0.90; built-up areas: 0.78). However, only few species are found here. This pattern supports that some highly endangered species are pre-adapted (sensu McDonnell & Hahs, 2015) to intensively designed and novel urban biotope. Examples of rare species that are adapted to highly disturbed sites are *Chenopodium murale*, *Filago minima* and *Sagina apetala*.

Within the strongly anthropogenic biotope classes, ruderal sites had the most populations but also the lowest population survival rate (0.61). While novel urban ecosystems harbour many endangered plant species in Berlin (Kowarik & von der Lippe, 2018; Planchuelo et al., 2019), population survival seems to be limited in ruderal sites that are most prominent on vacant land. This may relate to the increased construction activities in Berlin during the last decades, which affect vacant land directly and indirectly. Alternatively, succession towards forest in these biotope classes may impair the habitats of rare ruderal species that usually rely on open habitats (Kattwinkel, Strauss, Biedermann, & Kleyer, 2009).

Grasslands cover only 5% of the area of Berlin (SenStadtUm, 2014), but hosted the second highest number of populations, with an intermediate survival rate of 69%. This confirms the importance of urban grassland for biodiversity conservation (Fischer et al., 2013; Kendal et al., 2017; Klaus, 2013) at the population scale. Better survival rates compared to forests may result from the long tradition of care in grassland biotopes while appropriate measures for shaded forests might be less commonly applied.

4.3 | Proximity to (semi-)natural ecosystems

The importance of natural remnants for urban biodiversity conservation is well established (e.g. Godefroid & Koedam, 2003). Accordingly, it has been found that nearby conservation areas had a positive effect on the occurrence of endangered plant species in the city of Prague (Jarošík et al., 2011). Our findings build on this by demonstrating that population survival of endangered plants is

negatively related to the distance between the population and the nearest natural remnant. Several complex interacting factors may contribute to this finding. Assuming that remnant sites within protected areas harbour many endangered species, the probability of successful dispersal increases with decreasing distance. These remnant populations could serve as a source for external populations, therefore reducing local extinctions. At closer distances to natural remnants, there is a higher chance of having similar site conditions (e.g. soils, hydrology), thus benefiting the endangered species dependent on these environmental features. Indeed, a companion study showed that populations of endangered plant species were spatially dependent on natural remnants—except for populations in novel ecosystems, that is, in settings with starkly differing site conditions (Planchuelo et al., 2020a). Our findings thus support conservation strategies that encourage the protection of large areas around natural remnants in formally protected areas—not only as a buffer but also as potential habitats for endangered species.

4.4 | Species traits

While none of the metric plant traits were retained in the tree model as predictors of population survival, indicator values for soil humidity requirements and the CSR strategy types differentiated three groups of species with distinct survival rates (Figure 3). The first split of the model delineated a group of species with the highest requirements on soil humidity and a rather low population survival. This corroborates previous findings on low performance of wetland species in urban areas (e.g. Knapp et al., 2010). In Berlin, wetland species are particularly prone to extinction due to large-scale groundwater subsidence caused by extensive sealing and groundwater withdrawal (Seitz et al., 2018; Sukopp, 1990). One example from our study is *Ranunculus lingua*—a highly endangered wetland species with a low population survival (17%). Climate change may further impair population survival of species that require high soil humidity as Berlin has increasingly experienced periods of higher temperatures and less precipitation over the past 20 years (Cubasch & Kadow, 2011), and future climates may continue this trend.

The second predictor in the model, CSR strategy, split the remaining species into two groups: one with medium survival rates, characterized by ruderal and stress tolerant strategies, and a second with the highest survival rates of species assigned to the competitive strategy. While competitive species usually have higher prospects of long-term survival (Chocholoušková & Pyšek, 2003; Knapp, Kühn, Schweiger, & Klotz, 2008; Knapp, Kühn, Wittig, et al., 2008), it is surprising that the ruderal strategy type does not promote survival in urban environments. This is probably linked to the elevated risk of local extinction in ruderal habitats that are often subject to habitat transformation as described above and the fact that competitive species are associated with locations with high nutrient levels (Grime, 1977), a feature of many urban sites. Additionally, because our methodology did not allow us to track the appearance of new populations, ruderal plants that had dispersed into nearby sites might have been recorded as extinct, thus biasing our results against ruderal species.

4.5 | Practical implications

This study supports the role of cities for preserving biodiversity by demonstrating opportunities for population survival of endangered plants in different urban settings. Yet, we also revealed considerable challenges since 36% of the populations of endangered plant species went locally extinct during a period of <10 years. Moreover, negative effects of urbanization dynamics (i.e. increasing impervious surface) in adjacent areas indicate extinctions debts since urbanization is progressing in Berlin, as in many cities.

Importantly, population survival rate differed between biotope classes, and with respect to some traits of the endangered species. These results can support conservation policies, management and research. Examples include the selection of species with particular traits for re-introductions to suitable urban habitats and priority setting in managing populations of target species in different urban settings. Generally, our study illustrates the usefulness of allocating limited conservation resources to population monitoring, more so considering the recent claim on the importance of long-term monitoring in anthropogenic systems (Haase et al., 2018; Pergl et al., 2019).

More specifically, the lowest survival rates in urban forests challenges current policies in forest management that aim to support the species composition and structure of semi-natural forests (SenStadtWo, 2019b). Our results support complementing strategies of forest management with approaches that mimic historical land uses to facilitate endangered species with high light requirements, for example, by thinning the canopy and shrub layer in parts of the forests.

The low population survival in bog- and wetland-species points to challenges in maintaining hydrological systems despite increasing constraints due to added effects of traditional drivers of decline (e.g. drainage) and climate change impacts. Since most wetlands are already protected areas in Berlin, our results also indicate limits in conserving *all* endangered species in urban environments.

Finally, the unexpectedly high population survival of a few endangered species in green areas or built-up areas suggests unexploited opportunities to re-introduce some pre-selected species to public greenspaces (Klaus, 2013; Pan et al., 2019). In summary, our study supports a wide range of conservation approaches within and outside protected areas in cities that cover natural and anthropogenic ecosystem types.

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AUTHORS' CONTRIBUTIONS

All persons entitled to authorship have been so named. All authors conceived the ideas, designed methodology and contributed to writing; G.P. processed the data; G.P. and M.v.d.L. analysed the data. All authors gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data are available via the Dryad Digital Repository: https://doi.org/10.5061/dryad.s1rn8pk4v (Planchuelo, Kowarik, & von der Lippe, 2020b).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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